
LIFE HISTORY PATTERNS AND BIOGEOGRAPHY: AN INTERPRETATION OF DIADROMY IN FISHES¹

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ABSTRACT

Diadromy, broadly defined here as the regular movement between freshwater and marine habitats at some time during their lives, characterizes numerous fish and invertebrate taxa. Explanations for the evolution of diadromy have focused on ecological requirements of individual taxa, rarely reflecting a comparative, phylogenetic component. When incorporated into phylogenetic studies, center of origin hypotheses have been used to infer dispersal routes. The occurrence and distribution of diadromy throughout fish (aquatic non-tetrapod vertebrate) phylogeny are used here to interpret the evolution of this life history pattern and demonstrate the relationship between life history and ecology in cladistic biogeography. Cladistic biogeography has been mischaracterized as rejecting ecology. On the contrary, cladistic biogeography has been explicit in interpreting ecology or life history patterns within the broader framework of phylogenetic patterns. Today, in inferred ancient life history patterns, such as diadromy, we see remnants of previously broader distribution patterns, such as antitropicality or bipolarity, that spanned both marine and freshwater habitats. Biogeographic regions that span ocean basins and incorporate ocean margins better explain the relationship among diadromy, its evolution, and its distribution than do biogeographic regions centered on continents.

Key words: Antitropical distributions, biogeography, diadromy, eels, fishes, global biogeographic regions, life history, migration.

"The extremely slow growth of the larvae of the European eel is...an adaptation to the prolonged journey [to spawning grounds in the Sargasso Sea]. It is scarcely possible to understand this unique phase in the life cycle of the European eel on the hypothesis that the geographical conditions were formerly the same as now exist. But if Wegener's theory [of continental drift] be accepted, the explanation is simple. As the coasts slowly receded from one another the larval life of what became the European species was more and more prolonged by natural selection in correspondence with the greater distance to be traversed."

—Fulton (1923: 360)

Animals that migrate between marine and freshwater at some time during their life are diadromous, a term coined by American ichthyologist George S. Myers (1949a). Several categories of diadromy were defined or redefined (Myers, 1949a, b; McDowall, 1988)—anadromy, catadromy, and amphidromy—collectively referred to as diadromy herein. Some invertebrate taxa, such as atyid crustaceans and neritid gastropods, are also diadromous (e.g., Myers et al., 2000).

Thomas Wemyss Fulton (1855–1929) was a Scottish fisheries biologist best remembered today for his classic *The Sovereignty of the Sea* (Fulton, 1911), a treatise on the development of the notion of territorial waters. Fulton's life began in 1855, a few years before Charles Darwin's publication of *On the Origin of Species* in 1859, and ended in 1929, just as Alfred I. Wegener published the fourth edition of *Die Entstehung der Kontinente und Ozeane*, the proposal of a theory of continental drift. In his letter to *Nature*, quoted above, Fulton described a hypothesis for the evolution of catadromy in the European eel, *Anguilla anguilla* (L.), which incorporated modern concepts of panbiogeography. First, the earth and its biota evolved together, a tenet of botanist Léon Croizat (1958). Second, global biogeographic regions should be centered on ocean basins, not continents (Croizat, 1958; Craw et al., 1999: figs. 6–13). Third, following from the first two, migration patterns evolve in concert with geology, and these changes lead to lineage differentiation, here changes in length of larval period, and ultimately to what we recognize as

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speciation. When Fulton referred to "... what became the European species..." he postulated that there had been a widespread northern Atlantic lineage that, along with geological evolution of the Atlantic Ocean, differentiated to become the European eel in the eastern North Atlantic and the American eel, *A. rostrata* (Lesueur), in the western North Atlantic. *Anguilla anguilla* and *A. rostrata* are hypothesized sister lineages (Lin et al., 2001a, 2005; see below).

Other early 20th-century biologists adopted earth history to explain the evolution of migration patterns. Notable among ornithologists was Albert Wolfson of Northwestern University, Illinois, who, in 1948, wrote a lead article in *Science*, "Bird Migration and the Concept of Continental Drift," which correlated the increasing distances birds traveled with the separation of land masses and their latitudinal shift. Nearly four decades later, Wolfson (1986) vividly recounted the negative and positive reaction to his correlation of bird migration and continental drift.

Many modern explanations for the evolution of migration and diadromy conflict with those of Fulton and Wolfson because, for the most part, they reject the coupled evolution of life and earth, at global and local scales, and rely exclusively on ecological and evolutionary models. For example "...the relative productivity or growth advantage of sea and freshwater habitats appears to be the key to [diadromy's] evolution. The productivity differential can probably explain why fish migrate across the sea-freshwater boundary, predict their direction of movement and account for where in the world diadromous species occur" (Gross, 1987: 21). Earth history was separated from biological history, in part as a return to center of origin explanations for geographic distributions as outlined by Matthew (1915) in his influential, often reprinted "Climate and Evolution" (see Nelson & Ladiges, 2001). Equally influential was Myers, who classified fishes in ecological categories for the purposes of biogeography. A decade before he defined diadromy, Myers (1938) proposed divisions of freshwater fish taxa based on their ability to tolerate saltwater: freshwater fishes, including primary division freshwater fishes (no salt tolerance), secondary division freshwater fishes (some salt tolerance), and peripheral or migratory fishes (diadromous) versus marine fishes (salt tolerant). These categories have been incorporated into fish biogeography and are still used broadly today (e.g., McDowall, 1988; Helfman et al., 1997; Berra, 2001). (The category of primary division freshwater fishes was modified by paleontologist Colin Patterson [1975], who recognized archaolimnic taxa, those inferred to have originated and always lived in freshwaters, and telolimnic, those living in freshwater now, but not necessarily through-

out their history. These two categories have been used almost exclusively by paleoichthyologists [e.g., Hilton, 2003].) Following Myers's ecological classification, the distribution of primary division freshwater fishes has been interpreted with respect to earth history (viz. Darlington, 1957), whereas the distribution of secondary division freshwater fishes, peripheral fishes, and marine fishes has largely not (e.g., Briggs, 1974, 1995; but see Springer, 1982; Parenti, 1991; Mooi & Gill, 2002; Nelson, 2004).

Accepting Myers's ecological categories precludes the comparison of distribution patterns among diadromous, freshwater, and marine fishes: "It is plainly evident that a fish which can swim through sea water from one river mouth to another is not of much use in studies of terrestrial zoogeography" (Myers, 1938: 343). And so it was believed by Myers and contemporaries (e.g., Herre, 1940) and subsequent generations of biogeographers. Adhering to Myers's philosophy, biogeography of marine and freshwater fishes on a global scale remains largely independent. Textbooks and courses have traditionally drawn the line, contrasting *Zoogeography of the Sea* (Ekman, 1953) and *Marine Zoogeography* (Briggs, 1974) with *Zoogeography of Fresh Waters* (Bănărescu, 1990, 1992, 1995), for example. More general texts, such as *Zoogeography: The Geographical Distribution of Animals* (Darlington, 1957), *Global Biogeography* (Briggs, 1995), or *Biogeography, an Ecological and Evolutionary Approach* (Cox & Moore, 2005), likewise have divided their attention between marine and freshwater taxa.

The arguments for dispersal (e.g., Gross, 1987; McDowall, 1970, 1988, 2001, 2002; Berra et al., 1996; Keith, 2003), vicariance (e.g., Rosen, 1974; Croizat et al., 1974), or some combination of the two (e.g., Choudhury & Dick, 1998) as explanations for the distribution of diadromous taxa, especially the antitropical salmoniform fishes, have been debated extensively. Likewise, broad geographic ranges have been interpreted as explicit evidence of dispersal (e.g., McDowall, 2001, 2002), of vicariance (e.g., Rosen, 1974), or of either dispersal or vicariance (Leis, 1984). Fulton's explanation for *Anguilla* Schrank distribution (above) will not convince a dispersalist to embrace vicariance or a vicariance biogeographer to adopt dispersalist explanations, as each represents a particular view of the relationship between the organism and the environment in forming biogeographic distributions.

Cladistic biogeography (viz. Nelson & Platnick, 1981; Humphries & Parenti, 1986, 1999; Crisci et al., 2003) puts primary emphasis on the phylogenetic relationships among organisms, not their physiological or ecological requirements, to discover distribution

patterns. Cladistic biogeographers do not ignore ecology (viz. Wiens & Donoghue, 2004), but, rather, are explicit in interpreting ecology or life history patterns within the broader framework of phylogenetic patterns (e.g., Sparks & Smith, 2005). Detailed reviews and commentaries on the systematics, biology, and distribution of diadromous fishes, largely within the dispersalist framework, have been provided by New Zealand ichthyologist Robert M. McDowall (e.g., 1970, 1987, 1988, 1992, 1993, 1997a, b, 2001, 2002, 2003). I have argued previously that the distribution of each genus of diadromous gobies of the subfamily Sicydiinae (family Gobiidae) may be described by the ocean basins in which it lives and, further, allopatry may be recognized at the generic level: the eastern Pacific and Atlantic *Sicydium* Valenciennes does not overlap with its sister genus *Sicyopterus* Gill in the Indian Ocean and western and central Pacific (Parenti, 1991; Parenti & Thomas, 1998).

My purpose here is to reinterpret the phylogeny and global distribution of fishes, both freshwater and marine, within a cladistic biogeographic framework to ask if, and if so, how, the biology and ecology of diadromous fishes are related to their distribution patterns and to competing models of earth history.

DIADROMY AND CLASSIFICATION OF FISHES

Table 1 lists the major groups of living aquatic vertebrates that we call fishes, the estimated number of species in each taxon, the number of species that live almost exclusively in freshwater, and the total number of species that enter freshwater during some phase of their lives (modified from Nelson, 2006: 4–5). Diadromous species are included in the last column, which also enumerates those species that do not undergo regular habitat migrations but are euryhaline, such as cyprinodontiform killifishes (see, e.g., Rosen, 1973). An estimated 225 species are diadromous (McDowall, 1992; Nelson, 2006). Not all diadromous species are obligately so (McDowall, 2001), precluding a precise enumeration of such taxa.

A large proportion of diadromous species is concentrated among inferred basal lineages: lampreys (Petromyzontiformes), sturgeons (Acipenseriformes), eels (Elopomorpha), herring (Clupeomorpha), and salmon (Protacanthopterygii), as noted by McDowall (1988, 1993) and others, and many species in these lineages are euryhaline. Many, but not all, diadromous fishes are also antitropical or bipolar, distributed in the northern boreal and/or the southern austral zone, and absent from the tropics, again as noted by McDowall (1988, 1993) and others. Salmoniforms and osmeriforms (Protacanthopterygii; Rosen, 1974: fig. 15), lampreys (Petromyzontiformes; Berra, 2001: 6, 8,

12) and some clupeomorphs (Nelson, 1986) have bipolar distributions, whereas sturgeons (Acipenseridae; Choudhury & Dick, 1998; Berra, 2001: 42) and sticklebacks (Gasterosteidae; Berra, 2001: 351) are boreal, for example.

EPICONTINENTAL SEAS: THE SETTING FOR BONY FISH EVOLUTION

Living actinopterygian (ray-finned) fish clades are the bichirs (Polypteriformes), sturgeons and paddlefishes (Acipenseriformes), gars (Lepisosteiformes), bowfins (Amiiformes), and the bony fishes (Teleostei; see Nelson, 2006). Relationships among these lineages have been debated by both morphologists and molecular biologists (e.g., Nelson, 1969a; Patterson, 1973; Wiley & Schultze, 1984; Inoue et al., 2003) and, for the purposes of this discussion, may be summarized by the cladogram of Figure 1.

Polypteriformes (e.g., Britz, 2004) live in African freshwaters. Fossil bichirs of Africa and South America are of Middle Cretaceous age (Nelson, 2006).

Acipenseriformes (Grande & Bemis, 1991) comprise the anadromous and freshwater circumboreal sturgeons, Acipenseridae, and the paddlefishes, Polyodontidae. There are two extant species of paddlefish, one in freshwater in North America and the other in freshwater and estuarine habitats in the Yangtze River and associated areas of China. Fossil paddlefishes date to the Lower Cretaceous from China (Berra, 2001). Sturgeons are an old lineage, known from at least the Middle Jurassic (175 million years ago [Ma]; Choudhury & Dick, 1998).

Lepisosteiformes includes one living family, Lepisosteidae (Wiley, 1976), which comprises two extant genera with seven species living in fresh, brackish, or marine waters in North and Central America and Cuba. Fossil gars are more broadly distributed throughout North and South America, Europe, Africa, and India (Wiley, 1976: fig. 69); they date from at least the Early Cretaceous (Janvier, 2007).

Amiiformes (Grande & Bemis, 1998, 1999) are represented by one living species, *Amia calva* L., distributed in freshwater habitats in North America. It is the single, living representative of the Halecomorphi, known from marine and fossil taxa dating to the Jurassic.

The ancestral habitat for bony fishes is inferred from the phylogeny and distribution of living and fossil basal actinopterygian taxa to be shallow epicontinental seas and their freshwater margins, including river deltas (Fig. 1). A reconstructed widespread ancestral range was illustrated for a subgroup of halecomorph fishes by Grande and Bemis (1999: fig. 6), who outlined the distribution on a map of present-day geography contrasted with that of the

Table 1. Classification of living aquatic vertebrates (non-tetrapods) or fishes, estimated number of species in each taxon, number of those that live almost exclusively in freshwater, and total number of those that enter freshwater at some time during their life (from Nelson, 2006: 4–5; Stiassny et al., 2004). The last column includes all of the species in the second column, plus those that are migratory (diadromous or euryhaline).

Taxon	No. of species	No. of freshwater species	Total no. of species that enter freshwater
Myxiniformes	70	0	0
Petromyzontiformes	38	29	38
Elasmobranchii	937	24	40
Chimaeriformes	33	0	0
Osteichthyes			
Sarcopterygii			
Coelacanthiformes	2	0	0
Ceratodontiformes	6	6	6
Actinopterygii			
Polypteriformes	16	16	16
Acipenseriformes	27	14	27
Lepisosteiformes	7	6	7
Amiiformes	1	1	1
Teleostei			
Osteoglossomorpha	220	220	220
Elopomorpha	857	6	33
Clupeomorpha	364	79	85
Ostariophysi	7980	7847	7858
Protacanthopterygii	356	127	152
Esociformes	10	10	10
Stomiiformes	391	0	0
Ateleopodiformes	12	0	0
Aulopiformes	236	0	0
Myctophiformes	246	0	0
Lampridiformes	21	0	0
Polymixiiformes	10	0	0
Paracanthopterygii	1340	21	24
Stephanoberyciformes	75	0	0
Zeiformes	32	0	0
Beryciformes	144	0	0
Gasterosteiformes	278	21	43
Synbranchiformes	99	96	99
Perciformes	10,033	2040	2335
Mugiliformes	72	1	7
Atherinomorpha	1552	1304	1352
Scorpaeniformes	1477	60	62
Pleuronectiformes	678	10	20
Tetraodontiformes	357	14	22
TOTALS	27,977	11,952	12,457

Early Cretaceous, 118 Ma. The present-day, disjunct transatlantic distributions are continuous when drawn across Cretaceous epicontinental seaways.

An area cladogram, or areagram, of halecomorphs indicating habitat, marine or freshwater (Fig. 2A), was used by Grande and Bemis (1999: fig. 7) to infer a marine ancestry for the group. This hypothesis results from optimizing habitat or, at the least, inferring that the habitat of the basal taxon is the ancestral habitat. It rests on the assumptions that the habitat has

changed (e.g., marine to freshwater), even when there may be no evidence for such a transformation, and that one or the other taxon of a sister group pair may be identified as basal (see Parenti, 2006; Santos, 2007; also see below). Without these assumptions, the ancestral habitat may be reconstructed as epicontinental seas, spanning marine and freshwater habitats (Fig. 2B). Likewise, bichirs in South America and Africa also represent a transatlantic distribution, that is, a remnant of the broader distribution pattern.

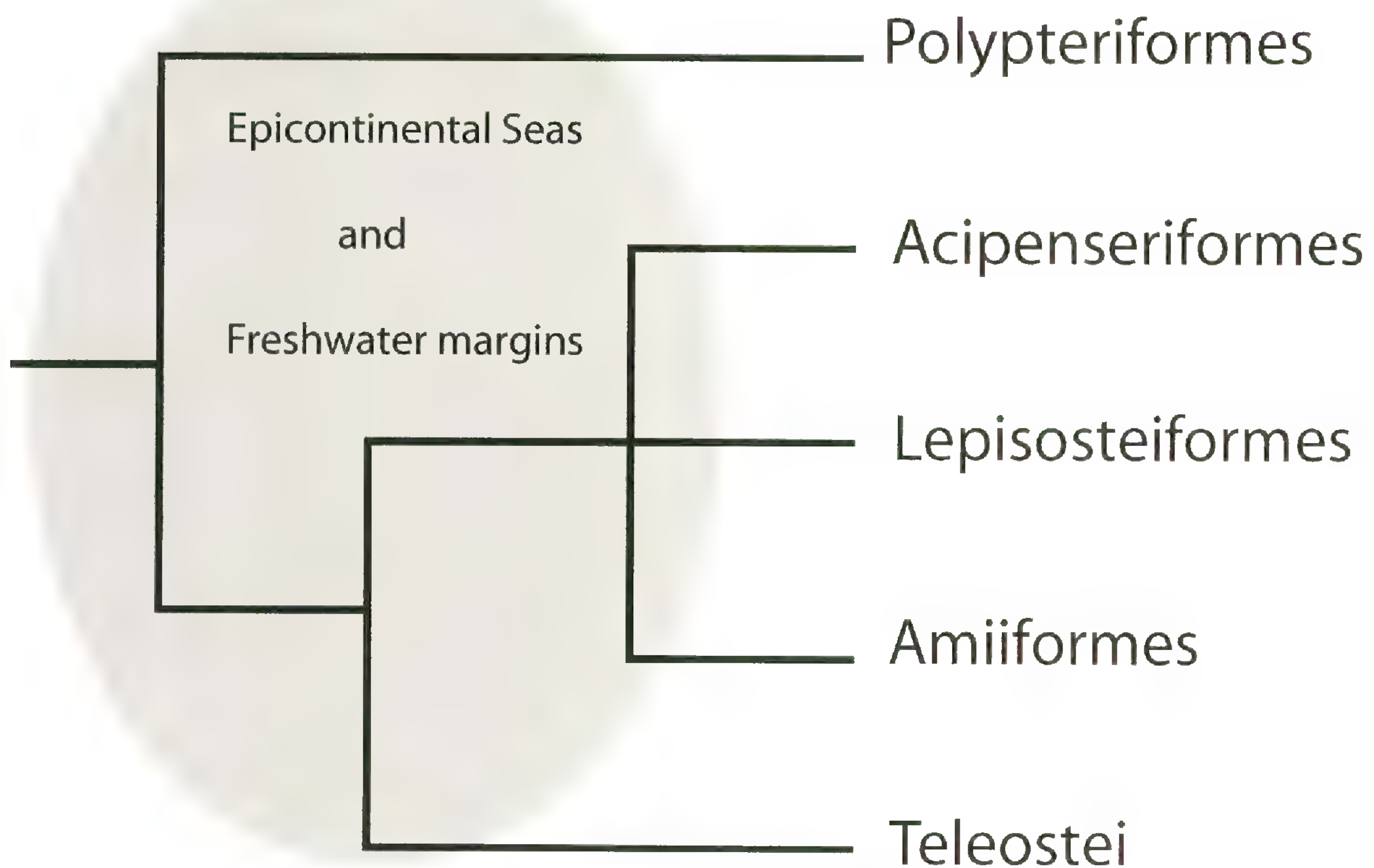


Figure 1. Hypothesized relationships among living actinopterygian clades, following Inoue et al. (2003) and Grande and Bemis (1999). The ancestral distribution is inferred to be throughout epicontinental seas and their freshwater margins.

Paddlefishes reflect transpacific relationships, as do other North American taxa (Grande, 1994a, b).

A lineage with marine and freshwater representatives (Fig. 3A) may be interpreted to have a marine and freshwater ancestral distribution (Fig. 3B). In a likelihood approach to reconstructing ancestral ranges of lineages, Ree et al. (2005: fig. 6c) also reconstruct a widespread ancestral range equivalent to that of Figure 3B when dispersal is considered unlikely, that is, when no a priori process is specified to explain the pattern (see also Ebach, 1999; Santos, 2007). “Ecologically variable ancestors” are analogous to “geographically widespread” ancestors (see Hardy, 2006: 13). (The method of Ree et al. [2005] does not correspond to other cladistic biogeographic methods, in part because it defines an area as a discrete geographic unit, not the organic areas of endemism that are defined by the ranges of the organisms that inhabit them [see Harold & Mooi, 1994].)

Our notion of freshwater and marine fishes comes, in large part, from the existence of speciose taxa that are today nearly all freshwater, such as the Ostariophysi (catfish, characins, minnows, and relatives) or Osteoglossomorpha (bony tongues), or from deep-sea marine orders, such as the Myxiniiformes (hagfishes), Chimaeriformes (chimaeras), Stomiiformes (dragonfishes), Aulopiformes (lizardfishes), Myctophiiformes (lanternfishes), and so on (Table 1). Osteoglossomor-

pha is the sister group to all other teleosts, all extant species of which live exclusively in freshwater (Nelson, 1969b, 2006; Table 1). It is not historically a freshwater lineage: marine Paleocene-Eocene fossils, such as the genus †*Brychaetus* Agassiz, are hypothesized to be nested in the osteoglossomorph cladogram in the family Osteoglossidae (Hilton, 2003). The oldest osteoglossomorph fossils are Middle Mesozoic, and Bănărescu (1995: 1162) acknowledged their long history and widespread ancestral distribution by proposing that Osteoglossomorpha is Pangean. Osteoglossomorpha, therefore, has both marine and freshwater representatives and is a freshwater group today because of widespread extinction of marine taxa. If the majority of species in a taxon are marine and just a handful are freshwater, it is often assumed that the group originated in marine habitats and several taxa dispersed to freshwater (e.g., Myers, 1938; Berra, 2001; Tsukamoto et al., 2002). The reverse is also assumed. Such an assumption is not an analysis of biogeographic data, but an implicit and untestable center of origin hypothesis (viz. Croizat et al., 1974).

Both Nelson (1973) and Patterson (1975) optimized habitat on areagrams to infer habitat of origin of osteoglossomorphs and came to different conclusions. For example, Patterson (1975: 162) asserted that “...if the conventional view of the history of

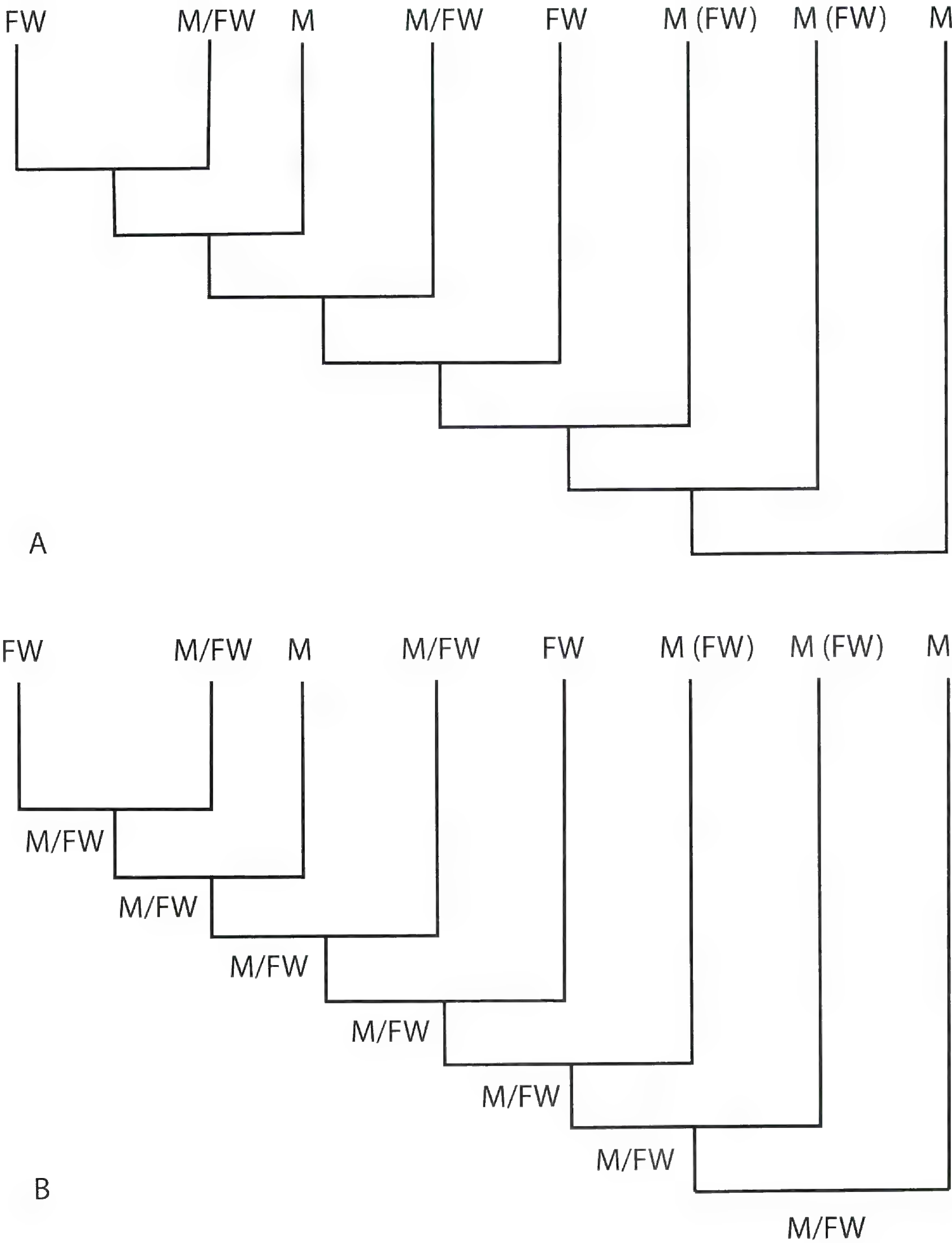


Figure 2. —A. Areagram of halecomorph habitats from Grande and Bemis (1999), who inferred a marine ancestry for the group. M/FW means distribution in marine and freshwater habitats; M (FW) means distribution mostly in marine habitats with some representatives in freshwater. —B. Reconstruction of nodes to infer a widespread marine/freshwater ancestral habitat, interpreted here as epicontinental seas and their freshwater margins.

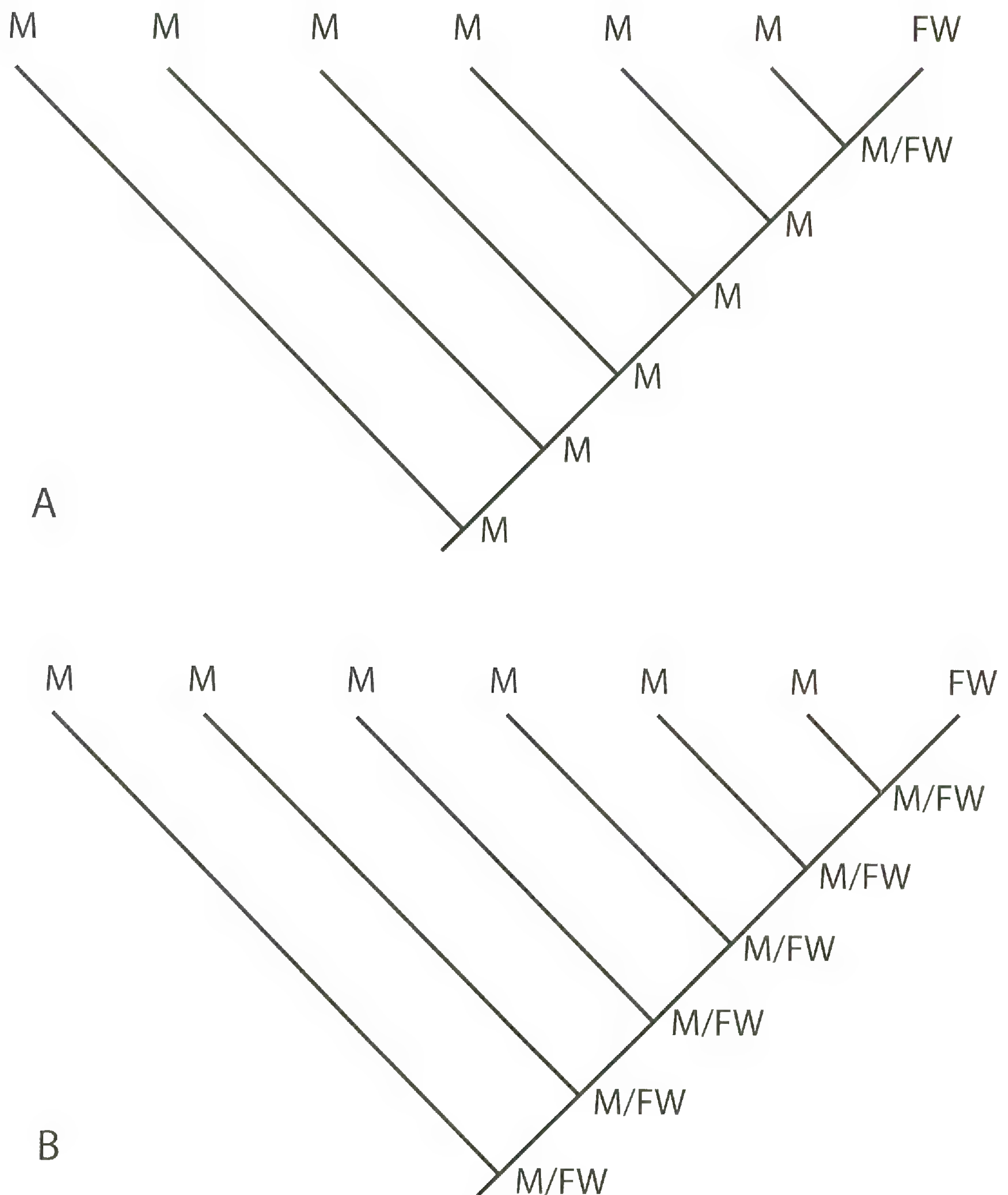


Figure 3. Hypothetical areagram representing taxa in marine (M) and freshwater (FW) habitats. —A. Optimization of nodes to infer a marine center of origin. —B. Reconstruction of nodes to infer a widespread marine/freshwater ancestral habitat.

Gondwana is accepted, marine origin of the Osteoglossomorpha is indicated.” Nelson (1973: 9), who read Patterson in manuscript, countered that “...the totality of evidence concerning the relationships and distribution of osteoglossomorphs, both fossil and Recent, indicates that †*Brychaetus* is secondarily marine,” that is, that osteoglossomorphs originated in freshwaters.

Even though Nelson later dismissed such arguments (e.g., Nelson, 1974; Nelson & Ladiges, 2001), they persist (see Parenti, 2006). Optimization of habitat on an areagram has been applied broadly to interpret the ecological and distributional history of lineages (see, e.g., Brooks & McLennan, 1991; McLennan, 1994). Optimization of habitat is often justified by the principle of parsimony, yet, in practice, can require

multiple hypotheses of switching between habitats (e.g., Baker, 1978). The distributional history of gobioid fishes, for example, was hypothesized by Thacker and Hardman (2005: 869): "... gobioids arose in freshwater, from a marine ancestor, then returned to marine habitats once or many times."

Whether diadromy or euryhalinity is a primitive or derived life history pattern for fishes has been debated seemingly endlessly (Tchernavin, 1939; Denison, 1956; Patterson, 1975; Griffith, 1987; McDowall, 1988, 1993, 1997a; Johnson & Patterson, 1996; Bemis & Kynard, 1997; Waters et al., 2000; see especially review in Janvier, 2007). The distribution of fishes throughout epicontinental seas, including along their margins, as proposed for basal actinopterygians, is in accord with numerous explanations for the evolution of solely freshwater or marine taxa from widespread diadromous or euryhaline ancestors. Suppression of the marine or of the freshwater life history phase of a migratory lineage could lead to evolution of solely freshwater or marine fishes, respectively, as speculated by Patterson (1975: 168–169). In addition to evolution of development, the roles of extinction and earth history have been recognized: isolation or stranding through changes in sea level or other vicariant events can result in a former euryhaline species being restricted to freshwater, for example (e.g., Choudhury & Dick, 1998; Waters et al., 2000; Heads, 2005a), a phenomenon termed "ecological stranding" (Craw et al., 1999). Widespread extinction of the earth's biota since the Upper Mesozoic has left just remnants of these formerly widespread distributions, "the ring on the bathtub" to paraphrase Heads (1990: 225). Isolation in one habitat or the other by stranding does not require or imply invasion of that habitat (see also Heads, 2005a). Some taxa persist in freshwater, others in marine habitats, and some in both.

EARTH HISTORY MODELS

Plate tectonics is the model used most often to interpret global distribution patterns with respect to earth history (e.g., Rosen, 1974; Patterson, 1975; Springer, 1982; Choudhury & Dick, 1998; Grande & Bemis, 1999). The model specifies an Atlantic Ocean expanding since the Mesozoic and supports vicariant explanations for transatlantic taxa, yet leaves biogeographers scrambling for similar explanations, such as migration of allochthonous terranes, for the distribution of transpacific taxa (McCarthy, 2003: 1556). A vicariance explanation of transpacific taxa finds geological support in the still-maligned theory of Expanding Earth, which specifies that the age of the Pacific Ocean is roughly the same as that of the Atlantic and Indian oceans (Shields, 1979, 1983,

1991, 1996; McCarthy, 2003, 2005). Biogeographic sister areas across the Pacific have complementary, matching geological outlines (McCarthy, 2003: fig. 3). That there are competing models of earth history endorses the view that biogeographic patterns should be discovered, then interpreted with respect to these models, rather than the models a priori specifying biogeographic patterns (Ebach & Humphries, 2002).

Minimal divergence times between lineages have been estimated using ages of fossils or a molecular clock and used to test hypotheses of dispersal versus vicariance (e.g., Rosenblatt & Waples, 1986; Sanmartín et al., 2001; Burridge, 2002, to cite just three examples). Minimal estimates from sequence data have been interpreted as absolute, thus calling into question earth history—Plate Tectonics or Expanding Earth—interpretations of distribution patterns (e.g., de Queiroz, 2005). This interpretation has been countered by Heads (2005b), Parenti (2006), and others, continuing a long debate within biogeography that was revived with the advent of molecular techniques (see especially Nelson, 2004). Teleost as well as basal actinopterygian lineages are old enough to be interpreted within earth history models. Fossils of living teleost lineages date from about 150 Ma in the Upper Jurassic, and teleosts as a clade are estimated to be at least of Triassic age (Janvier, 2007; see also Benton & Donoghue, 2007). Differentiation is also ancient: tetraodontiforms, nested within the apomorphic percomorph clade, are represented by fossils from the Upper Cretaceous of Slovenia, Italy, and Lebanon, the oldest of which dates from 95 Ma (Tyler & Sorbini, 1996).

DISTRIBUTION PATTERNS OF DIADROMOUS FISHES

Historical biogeographic patterns may be complex, and are, by definition, hierarchical. They are characterized by repeated elements that have become the basis of broadly recognized global distribution patterns (Croizat, 1958, 1964) that may be expressed in a classification (Fig. 4): Atlantic, Indian Ocean, (Pacific, Antitropical), or by fragments or composites of these areas. One stated aim of historical biogeography is to develop a standard language or nomenclature for global distribution patterns (e.g., Morrone, 2002) including their fragments. Fragmentation may be caused by extinction, which has left remnants of formerly complete distribution patterns, such as a lone freshwater representative of a taxon once living broadly in marine and freshwater habitats. These remnants have been used to interpret, and misinterpret, the distributional history of taxa (see Heads, 2005a, b; Nelson & Platnick, 1981; Nelson & Ladiges, 1991, 1996; also see below).

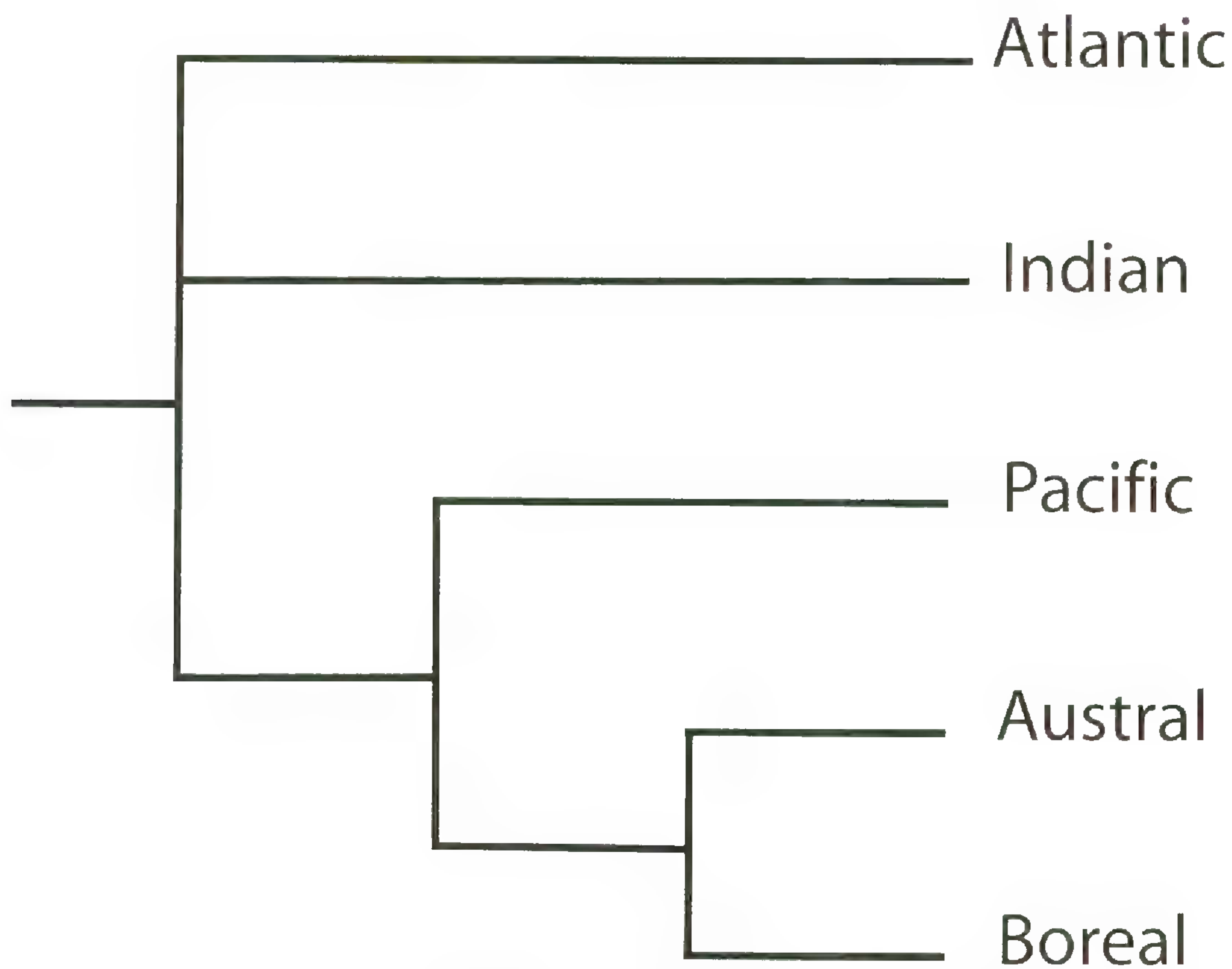


Figure 4. Areogram or classification of Croizat's (1958) and Craw et al.'s (1999) global biogeographic patterns, following Nelson and Ladiges (2001: fig. 8b).

The distribution of antitropical or bipolar taxa has been interpreted with regard to evolution of the Pacific Basin (e.g., Humphries & Parenti, 1986, 1999; Nelson, 1986). In a recent discussion of the evolution of diadromy among fishes of the southern oceans, McDowall (2002: 208) acknowledged but did not discuss bipolarity. He divided fishes of New Zealand into two kinds: those with close relatives throughout the southern oceans, such as lampreys and galaxioids, both groups bipolar, and those that he inferred, a priori, to be part of another global pattern: "Anguillid eels and gobiid [fishes] have *nothing in common* with the southern cool temperate fish fauna regarding historical origins, distributions and relationships. They are probably not Gondwanan and yet, anguillids and gobiids express a series of relationships and distributions between the faunas of eastern Australia and New Zealand that are *essentially the same* as those seen in southern families" (*italics added*) (McDowall, 2002: 212–213). Sharing a pattern implies sharing a history: I examine the distribution of eels and gobies to ask if they have anything in common with the southern cool fish fauna—in other words, whether they conform to the same global as well as local patterns.

PHYLOGENY AND DISTRIBUTION: EELS

Eels of the genus *Anguilla* are catadromous (Myers, 1949a): adults live in freshwater streams and migrate to marine spawning grounds (Tesch, 1977; Smith, 1989a,

b). Phylogenetic relationships among the 19 extant taxa (Fig. 5) were hypothesized using molecular data by two research groups (Lin et al., 2001a, b; Aoyama et al., 2001), and these two sets of analyses were contrasted and compared with morphology (Lin et al., 2005). An areogram of *Anguilla* taxa, with taxon names of Figure 5 replaced by a brief description of distributional limits, is given in Figure 6. Another molecular phylogeny based on whole mitochondrial genome sequences was published by Minegishi et al. (2005).

Anguilla species are associated with all continents, except Antarctica, and do not live in the eastern Pacific or South Atlantic (Berra, 2001). Distribution of anguillid eels has largely been interpreted within a dispersalist paradigm (e.g., Harden Jones, 1968) and, recently, to conflicting ends (Heads, 2005a: 700): Lin et al. (2001a, b) put the center of origin of eels in the southwest Pacific and proposed dispersal eastward across the Pacific and further across the Central American Isthmus to enter the Atlantic Ocean, whereas Aoyama et al. (2001), Aoyama and Tsukamoto (1997), and Tsukamoto et al. (2002) hypothesized dispersal from a center of origin near Borneo, westward through an ancient Tethys Sea to the Atlantic Ocean. Both of these explanations were rejected by Minegishi et al. (2005: 141), who concluded that "...the present geographic distribution [of eels of the genus *Anguilla*] could be attributed to, for example, multiple dispersal events, multidirectional dispersion, or past extinctions, etc."

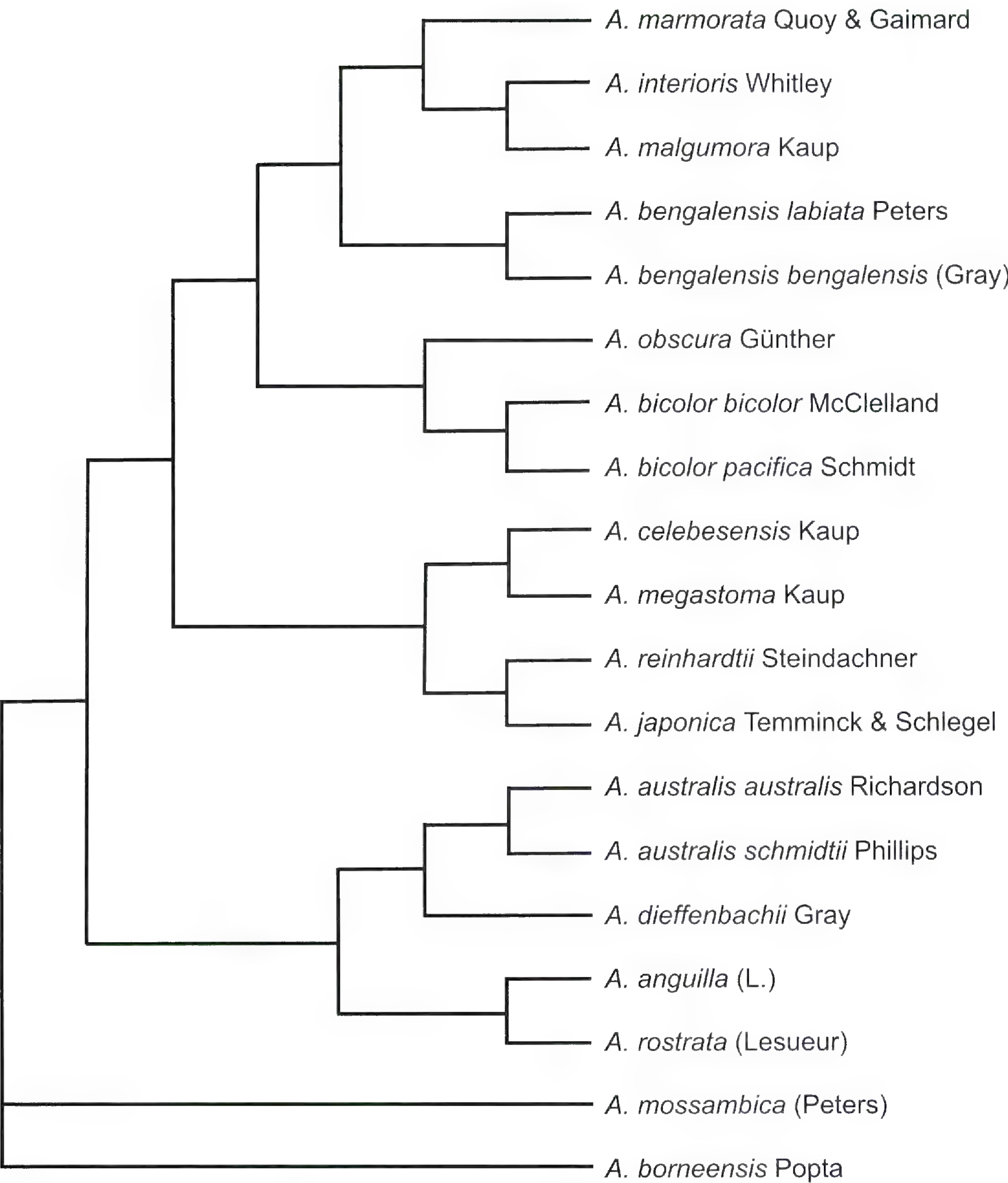


Figure 5. Cladogram of relationships of eels of the genus *Anguilla*, following Lin et al. (2001a). Branch lengths are arbitrary. *Anguilla malgumora*, as used by Lin et al., is a synonym of *A. borneensis*, the species name used by Aoyama et al. (2001) and Minegishi et al. (2005). Spelling of species names and authors follows Eschmeyer’s online catalog (<http://www.calacademy.org/research/ichthyology/catalog/>), accessed on 19 October 2007.

Panbiogeographers have long endorsed the view that the distribution and evolution of eels of the genus *Anguilla* may be interpreted with respect to earth history, specifically evolution of a Tethys Sea biota (Croizat, 1958), and dismiss ad hoc dispersal hypotheses (see Heads, 2005a). Cladistic biogeographers endorse the panbiogeographic view and add relationships among areas, as interpreted from phylogenetic hypotheses, as a framework for further refinement of distributional history patterns. Rather than optimizing areas, the information in the areagram of *Anguilla* taxa (Fig. 6) may be summarized by a variety of methods, such as reduced area–cladograms or paralogy-free subtrees (Nelson & Ladiges, 1996), or by comparing it to the cladistic summary of Croizat’s (1958) global biogeographic patterns (Fig. 4). Notable

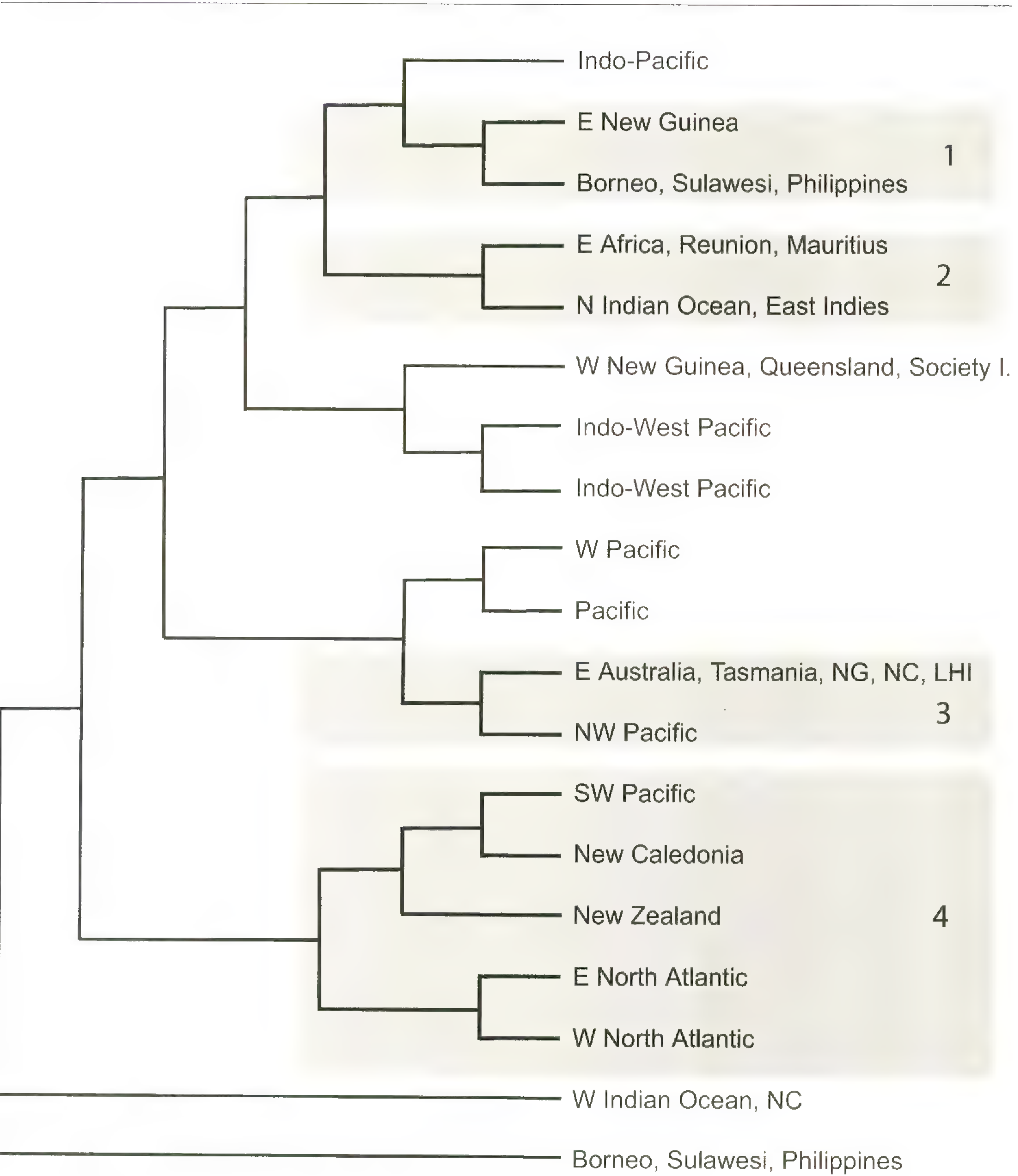


Figure 6. Areogram of *Anguilla* taxa, with taxon names of Figure 5 replaced by brief description of distributional limits. NG = New Guinea, NC = New Caledonia, LHI = Lord Howe Island. Shaded area 1: western margin of Pacific Basin; shaded area 2: Indian Ocean; shaded area 3: antitropical; shaded area 4: antitropical.

in the areogram of *Anguilla* (Fig. 6) are taxa distributed along the western margin of the Pacific Basin (shaded group 1), the Indian Ocean (shaded group 2), antitropical distributions, and antitropical taxa sister to Pacific taxa. Eels demonstrate one of the three-area relationships in the global biogeographic pattern (Fig. 4): Pacific (boreal, austral). Northwest Pacific taxa (boreal) are closely related to those from eastern Australia, Tasmania, New Guinea, and New Caledonia (austral, with additional elements from the western margin of the Pacific Basin; shaded group 3),

and these are, in turn, sister to a group of Pacific taxa. Another clade is also antitropical: the North Atlantic sister species (boreal) are closely related to a group of southwest Pacific, New Zealand, and New Caledonian taxa (austral; shaded group 4). Freshwater eels of the genus *Anguilla* have not been characterized as antitropical or bipolar, as antitropicality of fishes is seen largely as a phenomenon of strictly marine taxa (e.g., Nelson, 2006: 12). These remnants of antitropicality would likely not be identified without a hypothesis of phylogenetic relationships or without

the aim of identifying general patterns, rather than hypothesizing individual distributional histories.

Are anguillid eels ancient, like other antitropical taxa? Perhaps. A molecular clock estimate of 20 Ma for the beginning of *Anguilla* speciation was rejected by Minegishi et al. (2005: 141) as an underestimate because of fossil evidence: anguilliforms date from the Upper Cretaceous (113–119 Ma) and the genus *Anguilla* from the Eocene (50–55 Ma) (Patterson, 1993), both minimum estimates of the age of these lineages.

PHYLOGENY AND DISTRIBUTION: GOBIES

Gobioid fishes comprise over 2000 species distributed broadly in pantropical and temperate freshwater, estuarine, and marine aquatic habitats (Nelson, 2006). Because the vast majority of gobioids live in marine waters, they have been characterized as a marine group (e.g., Myers, 1938; Berra, 2001). Several subgroups, such as *Gobiomorphus* Gill, and the gobiid subfamily Sicydiinae are diadromous (e.g., Parenti & Maciolek, 1993; Keith, 2003). Phylogenetic analysis of sicydiine gobies and their relatives at the generic level (e.g., Parenti, 1991; Parenti & Thomas, 1998) has been offered as evidence that the repeated, recognizable biogeographic areas for gobioids are ocean basins, not continents (see also Springer, 1982; Gill in Lundberg et al., 2000).

Hypotheses of relationships among gobioids (e.g., Thacker & Hardman, 2005: fig. 1) are preliminary, yet, when combined with distribution, display remnants of global patterns (Fig. 4): Rhyacichthyidae, the sister group to all other gobioids, lives in the tropical western Pacific (Berra, 2001: 458), whereas Odontobutidae, sister to the remaining gobioids, exhibits a remnant boreal distribution, living in freshwaters of the northwest Pacific (Berra, 2001: 460). The southeast Australian and New Zealand *Gobiomorphus*, a goby genus that McDowall (2002: 213) characterized as “probably not Gondwanan,” is interpreted as having a remnant of an austral distribution; it is sister to a large gobioid lineage distributed throughout the pantropics. The fossil record of gobiids is scant; they date from at least the Middle Tertiary (Patterson, 1993).

Endemism of gobioids on islands or island groups is high, notably throughout the Indo-Pacific (Maugé et al., 1992; Parenti & Maciolek, 1993, 1996; Larson, 2001; Donaldson & Myers, 2002). Endemism throughout the marine realm is underappreciated in large part because marine species are defined traditionally as widespread (e.g., Gill & Kemp, 2002, fishes; Meyer et al., 2005, gastropods). Endemism may be under-recognized at both lower (species) and higher (genera) taxonomic levels. The lack of genetic structure among

populations of the five freshwater or amphidromous gobiid fish species living throughout Hawaiian streams (e.g., Chubb et al., 1998) prompted McDowall (2003) to conclude that they must have colonized Hawaii by long-distance, chance dispersal. Alternative explanations are plausible. Four of the five species are endemic to the Hawaiian Islands, as McDowall (2003: 705) acknowledged. Traditional island biogeography tells us that what inhabits an island or island group is what is able to physiologically and physically stand a long ocean voyage from the mainland (MacArthur & Wilson, 1967), although islands, as well as continents, are inhabited today by the remnants of once more diverse faunas. Islands and coastal zones support life that is able to withstand the wide swings in salinity, temperature, and so on (see also Heads, 2005a), and chief among that life is the diadromous or euryhaline taxon.

CONCLUSIONS

Biogeography of diadromous fishes is not about whether they are capable of surviving in the seas. They are, at least during some phase of their life history. It is not about whether diadromous fishes have marine or freshwater ancestors because all fish lineages have both. Biogeography of diadromous fishes is like that of all other taxa: a search for a pattern of relationships among endemic areas that conforms to or differs from general distributions of taxa worldwide. Eels and gobies, phylogenetically disparate and distinct diadromous taxa, reflect global biogeographic patterns. One can acknowledge this congruence, this conformity to a pattern, or one can ignore it. Predictions that may be made about distribution of diadromous taxa based on their life history are not necessarily corroborated by their phylogeny or their distribution patterns. The answer to “Why migrate?” is straightforward when earth history is considered: migration evolves as the earth evolves (see also Wolfson, 1948; Croizat, 1958; Heads, 2005a). Migration of diadromous species is “the result...not the cause” of their evolution (Wolfson, 1948: 30; see also Grehan, 2006). When interpreting the evolution of diadromy in fishes, or of any migration pattern, the relationship between phylogeny and distribution must be considered along with ecological patterns. Ecology, phylogeny, and distribution are inseparable (see also Heads, 1985).

The ability to live in both freshwater and marine habitats is interpreted as an ancestral life history pattern for fishes. The evolution of diadromy is tied to the evolution of ocean basins. Optimizing habitat on the nodes of an areagram to invoke an ancestral habitat, here marine or freshwater, is equivalent to

invoking a center of origin for areas. A repeated, general pattern among taxa that are not closely related and/or that differ in ecological requirements is most parsimoniously explained by the same events. There should be no separate global historical biogeography for marine and freshwater fishes. Proposing separate explanations for each prevents discovery of general patterns.

Today, we see but a remnant of the past distribution of life on earth. Global biogeographic patterns are the organizing framework for interpreting distributional and ecological history of both marine and freshwater taxa. Recognizing that anguillid eels have remnants of antitropical patterns, for example, is a first step toward accepting that their distribution may be classified along with that of other taxa, rather than a priori requiring a unique explanation.

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